Intra-specific variation in social organisation by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors

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Abstract: Previously, it was widely believed that each species has a specific social organization, but we know now that many species show intraspecific variation in their social organization. Four different processes can lead to intraspecific variation in social organization: (i) genetic variation between individuals owing to local adaptation (between populations) or evolutionarily stable strategies within populations; (ii) developmental plasticity evolved in long-term (more than one generation) unpredictable and short-term (one generation) predictable environments, which is mediated by organizational physiological effects during early ontogeny; (iii) social flexibility evolved in highly unpredictable environments, which is mediated by activational physiological effects in adults; (iv) entirely extrinsic factors such as the death of a dominant breeder. Variation in social behaviour occurs between individuals in the case of genetic variation and developmental plasticity, but within individuals in the case of social flexibility. It is important to study intraspecific variation in social organization to understand the social systems of species because it reveals the mechanisms by which species can adapt to changing environments, offers a useful tool to study the ultimate and proximate causes of sociality, and is an interesting phenomenon by itself that needs scientific explanation.

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Previously, it was widely believed that each species has a specific social organisation, but we know now that many species show intra-specific variation in their social organisation. Four different processes can lead to intra-specific variation in social organisation: 1. Genetic variation between individuals due to local adaptation (between populations) or evolutionary stable strategies within populations. 2. Developmental plasticity evolved in long-term (more than one generation) unpredictable and short-term (one generation) predictable environments and is mediated by organisational physiological effects during early ontogeny. 3. Social flexibility evolved in highly unpredictable environments and is mediated by activational physiological effects in adults. 4. Entirely extrinsic factors such as the death of a dominant breeder. Variation in social behaviour occurs between individuals in the case of genetic

variation and developmental plasticity, but within individuals in the case of social flexibility. Intra-specific variation in social organisation is important to study to understand the social systems of species because it reveals the mechanisms by which species can adapt to changing environments, it offers a useful tool to study the ultimate and proximate causes of sociality, and it is an interesting phenomenon by itself that needs scientific explanation.

Key words: social system; alternative reproductive tactics; population; frequency dependent selection; evolutionary stable strategy; striped mouse

1. INTRA-SPECIFIC VARIATION IN SOCIAL ORGANISATION

Understanding variation in social systems between species has long been one of the main aims in evolutionary biology (1-5). The social system of a species consists of the social organisation (the composition of groups), the social structure (describing who interacts with whom) and the mating system (6). Formerly, it was widely assumed that one species had one fixed form of social organisation. Divergence of single individuals from the species-specific pattern of social behaviour was often treated as noise in the data set. However, in the 1980s it was realized that variation in social systems occurs in many species, either between or within populations (7, 8).

Presently, the phylogenetic approach to understanding the evolution of different social systems is flourishing (9-11), but it requires each species to be categorised correctly with regard to its social organisation. However, apart from the standard categories (e.g. solitary, pair-living, multi male multi female species), there is no category for socially variable species. But to understand variation in social systems between species, it is important to understand the variation within species (7, 12). Here I focus on the social organisation, i.e. the composition of groups, because this is the parameter most easily measured in field studies, and because it influences the mating system, the social structure and thus the social system (6, 13).

Intra-specific variation in social organisation offers a unique opportunity to study the ultimate and proximate causes of social traits without any confounding phylogenetic effects (14, 15). Understanding the different mechanisms that underlie intra-specific variation in social organisation will also help us to understand how and whether species can adapt to changing environments, which would also inform conservation efforts. Finally, intra-specific variation in social organisation is itself an interesting phenomenon that needs scientific explanation both from the ultimate and the proximate perspective (7, 15).

While the occurrence of intra-specific variation in social organisation has received significant attention and acknowledgement recently, the focus has been on the associated ecological factors (13, 16, 17). Additionally, we need to understand the different proximate and evolutionary mechanisms that arise from these ecological factors. While many examples of population differences in social organisation exist (7), the underlying processes are typically not known. The aims of this review are to present an overview of the four processes that bring about intra-specific variation in social organisation (Fig. 1), and to critically evaluate the ecological (extrinsic) and physiological (intrinsic) factors that bring about this variation.

2. GENETIC VARIATION

Individuals of a species can differ genetically from each other in a way that influences their social behaviour (18, 19), such as their ability to form pair-bonds and social bonds, and their propensity to show parental care (20, 21). These individual differences in genotype influencing social behaviour could contribute to intra-specific variation in social organisation, both between and within populations.

If the environments of two populations of the same species differ in important aspects such as climate, availability of resources, pathogens, or the occurrence of other competing species, then natural and sexual selection can differ between populations, leading to local adaptations. For example, if the carrying capacity and thus population density differs between populations due to environmental factors, different social tactics might evolve in the two populations. Another example would be the benefits of maternal / parental and bi-parental care (22), which can vary with changes in food availability, availability of mating partners and ambient temperature (23). Local adaptation might then result in genetic differences between populations regulating the expression of social behaviours, which can cause the social organisation of the two populations to differ. For example in prairie voles (*Microtus ochrogaster*) most individuals in some populations are pair-living, whereas the majority of individuals in other populations are solitary. Those two model types of social organisation might represent genetic adaptations to different environments (24) (but see also (25)).

Genetic variation could also contribute to variation in social organisation within populations. If the variation in social organisation occurs between generations, this could be due to frequency-dependent or fluctuating selection, such that different genotypes prevail at different times within the population. If variation in social organisation occurs at the same time, this might be due evolutionarily stable strategies (ESS) that are genetically determined (26). In this case, two or more genetically determined strategies exist within the population that have the same fitness and a higher fitness than any alternative strategy (1). Such ESS have been documented in the case of alternative reproductive tactics (ARTs). In side-blotched lizards (*Uta stansburiana*) three male tactics exist that are genetically different and maintained via frequency-dependent selection (27). Genetically determined ARTs that could represent ESS occur in several species of fish (28), lizards (27), in ruffs (*Philomachus pugnax*; (29), and in the isopod *Paracerceis sculpta* (30). In fire ants (*Solenopis invicta*) the number of breeding queens per colony is determined by the single gene Gp-9, with one queen (monogynous social organisation) when only the B-allele is present, but multiple queens (polygynous social organisation) when the b-allele is present as well (31).

The existence of male ARTs alone might not change the social organisation unless females also show ARTs (15), but only in a few species do both sexes show ARTs. The extent to which genetic differences can explain intra-specific variation in social organisation is not well understood, maybe because most studies focussed on male ARTs within one population, which is easier than making comparisons between populations. Still, genetic differences between populations due to local adaptation influencing social organisation might be common, and this could initiate ecological speciation (32).

3. PHENOTYPIC PLASTICITY

Phenotypic plasticity is the capacity of a specific genotype to produce different phenotypes (in behaviour, physiology or morphology) in response to different environmental conditions, including the social and pre-natal environment (33). Phenotypic plasticity evolves when (i) the environment of a population varies between or within generations, (ii) individuals can use reliable environmental cues indicating (iii) which phenotype has the highest fitness, meaning that (iv) different phenotypes have different fitness in different environments and (v) no phenotype exists that has the highest fitness in all environments (summarised by (34)).

Phenotypic plasticity can occur early in development and lead to permanent changes of the phenotype, or it can be reversible, which often occurs in adults. The first phenomenon has been called developmental plasticity, the second one phenotypic flexibility (35). Different physiological mechanisms exist for these two kinds of plasticity, which also suggest that different evolutionary forces are at work.

(a) Developmental plasticity

In the case of developmental plasticity, variation is due to environmental variation activating alternative developmental pathways of one genotype (35). Developmental plasticity is non-reversible, making it empirically difficult to differentiate it from genetic variation between individuals. This can be best achieved by experimental studies in captivity testing for an influence of the environment on the phenotype. If environmental manipulation has no influence on the ratio of alternative phenotypes produced, genetic variation is likely to be the cause (36). If the environment significantly influences the resulting phenotype, developmental plasticity is likely to be at play (37). If in common garden experiments the observed differences in social organisation between populations disappear in the common garden, then developmental plasticity would be the explanation for the differences observed in nature.

Developmental plasticity is a response to the early environment within which an individual develops and in which it later grows up. For this, some cues of the current environment must reliably predict the future environment in which the same individual will reproduce, and this predictability must have occurred in the past when developmental plasticity evolved. As such, developmental plasticity enables the development of alternative adaptive phenotypes that have a higher fitness on average than any fixed phenotype. Typically, the environmental influence is during early development (pre- and / or postnatal), later affecting the phenotype of adult breeding individuals. This influence can occur before birth, for example due to the position in utero between male or between female siblings in rodents, and the resulting organisational effects due to the steroid hormones originating from the siblings (38). In rodents, maternal effects significantly influence stress response and social behaviour (39), which is an adaptive response to specific environments (40, 41). Developmental plasticity can also occur via environmentally induced changes in DNA methylation and as such represent epigenetic effects, causing phenotypic diversity (42).

If the environment of a population changes consistently, the development of the nervous system, and thus ultimately the social behaviour of this generation could significantly differ from that of other generations. Similarly, the environments of two different populations of the same species can differ significantly, inducing different developmental pathways, leading to intra-specific variation in social organisation. However, I am not aware of any empirical studies demonstrating the importance of developmental plasticity for intra-specific variation in social organisation, which could well be due to researchers not addressing the necessary research questions.

(b) Social flexibility

Social flexibility describes the phenomenon that the social organisation of a species or population can change as a function of individuals reversibly changing their social tactics in response to short-term changes of the environment. Thus, social flexibility focusses on changes in the population that are a function of individuals of both sexes reversibly changing their reproductive and social tactics (15)). Individuals modify their interactions with other individuals (social structure), with whom they mate (mating system), and consequently the composition of groups (social organisation) and thus the entire social system of the population. In the case of social flexibility, both males and females must have alternative reproductive tactics based on a single strategy (all individuals have the same decision rules) (43). Ecological constraints are one of the most important factors for the evolution of social flexibility (15, 17). These constraints can vary between years, often due to changes in population density, such that in some years philopatry and the establishment of large groups are favoured, in other years dispersal and solitary breeding (5, 15, 17). Within a population, often two or more forms of social organisation might exist, e.g. solitary and group-living individuals, or monogamous and polygynous groups.

One problem with the term social flexibility is confusion arising from the fact that most behaviours are flexible (reversible). Many researchers in animal behaviour use the term "flexible" to emphasize this characteristic feature of social behaviour. As such, "flexible" is a vague term without scale (which behaviour is flexible, which is not?) and neither a scientific phenomenon nor a theoretical concept. In contrast, the value of the term "social flexibility" is that it provides a conceptual framework that enables us to study ultimate and proximate factors of individual flexibility in social behaviour that leads to intra-specific variation in social organisation (15).

Interestingly, species that are flexible in their social behaviour might not show social flexibility but rather social specialisation. Primates are well known for their flexibility but have little social flexibility. This sounds contradictory, but means that their social behaviour shown towards other group members is flexible, but not the social organisation of their group. In primates, social organisation is most often species specific and barely varies within species, even though many species have large distributions across ecologically variable habitats (44, 45). Baboons (*Papio spec.*), for example, always form multi-male, multi-female groups, even though they occur in a wide range of habitats (45) and gibbons (*Hylobates spec.*) always live in monogamous family groups (45). Primates typically have a clear but flexible dominance hierarchy. Flexible social tactics enable them to respond to arising conflicts, environmental and social changes, stabilizing the social organisation of the group. Thus, flexibility in social behaviour enables primates to maintain their species-specific social organisation.

In contrast, social flexibility (population level) might arise in species that have little flexibility in social behaviour (individual level) towards other group-members. If conflict arises in these species, they might have to change their social organisation to resolve it. This is evident in the socially flexible African striped mouse (*Rhabdomys pumilio*) which can live solitarily, in single family groups or extended family groups (46). In this species, one can distinguish between non-breeding philopatric males and females, one breeding male and up to four breeding females per group (47). Surprisingly, no measurable dominance hierarchy exists and groups are highly egalitarian (48). If conflict occurs, no changes in dominance hierarchy are possible nor do submissive behaviours exist to resolve conflict. Instead, striped mice switch to a solitary lifestyle if conflict increases (46, 49). Social flexibility might thus arise from the absence of flexibility in social behaviour, making solitary living the only adaptive alternative to group living when inter individual conflict increases to a certain threshold level. In contrast, species with pronounced dominance hierarchies are able to adjust their social interactions with other individuals (social structure), enabling them to maintain their social organisation.

Social flexibility is predicted to be an adaptation to unpredictably changing environments, selecting for high phenotypic flexibility that is based on a broad reaction norm, not on genetic polymorphisms for specific tactics (15). The environment in which it evolved had to be less predictable than in the case of developmental plasticity, such that the environment in which an individual grows up does not provide significant information about the environment in which the same individual will reproduce. Thus, selection favours individuals that can change their social behaviour as adults. If this occurs in both sexes, the entire social organisation of a population can change. For example, both male and female striped mice can be highly sociable and form extended family groups, but the same individuals can switch to solitary living with very few if any social interactions (15, 46, 49). The fact that groups can exist even under conditions of low population density but split at the beginning of the breeding season (individuals leave the group) indicates that the individuals have a choice between group- and solitary living. Thus, the change in social organisation is a consequence of individual decisions (50) and not entirely due to extrinsic environmental factors (see below).

Social flexibility occurs in several species, including insects, birds and mammals (examples in Tab. 1). The most important factor selecting for social flexibility seems to be unpredictable fluctuations in population density influencing the extent of intra-specific competition. For example, in African striped mice, population density declined from one generation to the next from 32.4 to 1.5 mice/ha (factor of 21) due to an unexpected drought, and only a few generations (=years) later due to an unexpected and local increase of predation pressure (presence of a single wild cat) from 30.5 to 6.5 mice /ha (factor of 5) (46). In both cases, striped mice grew up under high population densities, when group-living and communal breeding were the best option, but they reproduced when population density was low and thus solitary breeding was the best option. Under high population density, inter-group competition in the form of territoriality is very strong (51) leading to small territories (52) and constrained dispersal, such that breeding in groups is favoured (46). However, living in groups can lead to female-female aggression and female infanticide (46) as well as sexual suppression of males by the dominant male (53), resulting in significant fitness costs that can be avoided by becoming solitary (49). Thus, under low population density, individual costs of inter-group competition are lower than costs of intra-group competition, making the switch from group- to solitary-living adaptive.

4. ENTIRELY EXTRINSIC FACTORS

Intra-specific variation in social organisation can also result solely from extrinsic factors (stochastic processes) leading to non-adaptive changes in social organisation. As such there can be no ultimate or proximate explanation for it. In this case the observed intra-specific variation in social organization is a direct consequence of a demographic interruption, and this variation is not due to an adaptive response of individuals to environmental change. Hereby the individuals will be forced to show flexibility in their behaviour to respond adaptively to the change (such as starting mate searching, dispersal), but this flexibility is not the reason for the observed intra-specific variation in social organisation that we want to explain but its consequence (Fig. 1).

In socially monogamous species, the natural death of one of the dominant breeders will change the social organisation not because the remaining family members chose this new social organisation, but simply because the disappearance of one breeder changes group composition. For example, Callitrichids, small New World monkeys, have been reported to show the highest degree of social flexibility in primates (45, 54), but in several species this might be due to social disruption (mortality of breeder) of the default social organisation of pair-living (12). Nevertheless, if such disruption occurs regularly and has significant fitness effects (55-57) it could function as an important selection pressure for social flexibility. On the other hand, the significant fitness costs associated with a deviation from social monogamy, especially female infanticide (55, 56), might explain the absence of social flexibility and instead a disposition to re-arrange social monogamy after social disruption. Thus, instead of the evolution of social flexibility, evolution of flexibility in social behaviour that promotes a return to a socially monogamous situation might have been favoured.

Individuals may be constrained to live solitarily when population density is very low, and constrained to be group-living when population density is very high, without giving individuals the *choice* to remain in a group or to become solitary. In some species, it is well known that the social organisation is rather inflexible and not influenced by population density. Obligate social species form groups even under very low population densities, for example lions (*Panthera leo*) in the Kalahari (58). On the other hand, some species like whistling rats (*Parotomys brantsii*) live solitarily even under very high population densities (59). Thus, while ecological factors are important in explaining intra-specific variation in social organisation, it is not clear whether these extrinsic factors alone are sufficient to explain differences between species.

5. PHYSIOLOGICAL MECHANISMS UNDERLYING INTRA-SPECIFIC VARIATION IN SOCIAL ORGANISATION

We know that the gene-environment interaction determines phenotypes (including behavioural phenotypes). Thus, changes in both genotypes and in the environment can induce changes in social behaviours. The four different processes that can explain intra-specific variation in social organisation are predicted to have evolved in different environments with different selection pressures (Tab. 2). The underlying physiological factors, themselves being the result of evolution, differ accordingly (Tab. 2). Here the concept of organisational *vs.* activational effects is important (60). Organisational effects occur early in development and are non-reversible, as in the case of sex determination in mammals (60). Activational effects typically occur in adulthood and are reversible, for example the activation of sexual behaviour by testosterone (60).

In species where genetic variation explains the variation in social organisation, two or more genotypes occur that cause different developmental pathways characterized by different organisational effects, such as in the case of genetically determined ARTs (36). In the case of developmental plasticity only one genotype occurs, but depending on the environment this can lead to alternative developmental pathways that will rely on different organisational effects, resulting in a determined, non-flexible adult phenotype (35).

Physiological mechanisms of social flexibility are expected to consist of activational, reversible effects such as environmentally induced neural activation or secretion of specific hormones or neuropeptides. The effects of many endocrine parameters on changes in social behaviour have been demonstrated, such as those of prolactin and steroid hormones on parental care (61), and those of testosterone on reproductive behaviour (62). Neuroendocrine changes, e.g. in the production and secretion of neuropeptides (oxytocin, vasopressin), have been demonstrated to be important too, but have been shown only in a few species because of the difficulties of assessing neuropeptides (63). Finally, activation of existing neuronal pathways and neural mechanisms of learning can be expected to be important, but are difficult to study and poorly understood. In sum, social flexibility is regulated by activational physiological mechanisms, enabling an adaptive and reversible response to unpredictable environments.

Genetically or developmentally determined neuronal pathways can be superior to flexible ones, because flexibility requires energy, time, and the opportunity to change (64). In the neurosciences, it is widely held that genetically fixed neuronal patterns are favoured under long-term environmental stability, but that flexibility will be favoured when there is significant environmental instability (65). Developmental plasticity is more advantageous than genetic determinism when change occurs predictably. Flexibility, by learning or by physiological activational effects, is favoured over genetically or developmentally determined pathways when change happens unpredictably. This is related to the Baldwin effect which states that while acquired traits cannot be inherited, the tendency to acquire traits can be inherited (66). Thus, the Baldwin effect describes the evolution of the ability to respond optimally to a particular environment. This is the result of selection for genes for plasticity and flexibility enabling adaptation to the current environment, rather than genes for a fixed phenotype (67). However, while the idea of the Baldwin effect is more than 100 years old and many studies have demonstrated how organisms rapidly respond both physiologically and behaviourally to changing environments, we still cannot easily link functional importance and inheritance of novel accommodations, i.e. the idea that natural selection sorts among developmental variants for genes enabling plasticity and flexibility (68). In other words: we do not know whether flexible genes *vs.* inflexible genes exist (but see (69)).

In the case of extrinsic factors alone causing intra-specific variation in social organisation, no specific physiological mechanisms exist that lead to the change of social organisation, which entirely depends on the environment. Instead, a stress response will be activated, leading to behavioural changes to return to the default social organisation (70).

6. FUTURE RESEARCH

While the four suggested processes offer an approach to study ultimate and proximate explanations for intra-specific variation in social organisation, many unanswered questions remain:

1. What are the benefits of having a narrow reaction norm (environmental canalization reducing environmental influence on the phenotype) versus having a broad reaction norm? Constraints for the evolution of phentotypic plasticity have received significant theoretical attention, and many studies addressed the costs (same phenotype of plastic genotype has lower fitness than of specialised genotype) and limits (plastic phenotype cannot produce the trait as well as the specialised genotype) of phenotypic plasticity (34,

71, 72). However, decades of research revealed that costs of phenotypic plasticity are surprisingly low (71, 73) and we still do not understand why so many species are specialists instead of being plastic generalists. Few if any empirical studies directly compared specialised *vs.* plastic species, asking under which circumstances can flexible species outcompete specialised ones and vice versa.

2. What environmental selection pressures lead to the evolution of developmental plasticity, which ones to the evolution of social flexibility? Theoretical models exists to explain the evolution of plasticity (developmental plasticity or flexibility) (34) as well as its costs, limits and constraints (71). If the current environment reliably predicts the future environment, developmental plasticity is predicted to evolve, but with increasing unpredictability social flexibility might evolve (Tab. 2), enabling a quick response that can be reversed if the environment changes again. This might be especially important in (1) highly unpredictable environments, and (2) in long-lived species, as predictability tends to decrease with increasing time in the future. In contrast, developmental plasticity resulting in an inflexible phenotype might reduce specific costs of plasticity, especially maintenance and information-acquisition costs: for developmental plasticity, individuals only need to acquire information about the information once in early development, when deciding which developmental trajectory to follow.

All four processes mentioned here are possible explanations for intra-specific variation in social organisation, but few studies have identified which one explains the pattern found in a specific population or species. In Tab. 3 I provide several predictions for the four different processes that can be used to determine which one explains the pattern of intra-specific variation in social organisation observed in a particular species. While writing this review, it became evident to me how little we know about the processes underlying intra-specific variation in social organisation. I wanted to include many empirical examples for the four possible processes, but apart from my own research topic – social flexibility – not much literature exists for the other processes. Of course, flexibility might be the most common process for intra-specific variation in social organisation and the other processes might be less important. Genetic variation and developmental plasticity might be important in the expression of individual differences in social behaviour (for example ARTs), but rarely explain intra-specific variation in social organisation. Entirely extrinsic factors might be the most overlooked process, because even in this case ecological factors do exist (stochastic mortality by a predator is ultimately also due to an ecological factor), and researchers in behavioural ecology are prone to see intra-specific variation as an adaptive response to a changing environment, without taking non-adaptive alternatives into account.

Environmental factors are important regulators of intra-specific variation in social organisation, and these factors have been studied extensively (1, 15, 17, 74, 75). For all four processes, the environment is a significant factor, either as a selection pressure (genetic variation), because the current environment determines the best tactic for the next generation but not for more distant generations (developmental plasticity), or because only the current environment determines the best tactic for the currently breeding individuals (social flexibility). Thus, to really understand both the ultimate reasons and the proximate causes of intra-specific variation in social organisation, we have to go further than focussing on the environmental factors. By a combination of only two studies one can differentiate between the four processes (Tab. 4).

The resilience of a species, population or an individual to environmental change depends on its ability to respond adaptively. To understand how species are able to adapt to changing environments we need to understand the different mechanisms of intra-specific variation in social organisation, which is the consequence of individual adaptive responses. If environmental change happens slowly, fluctuates predictably or if environments differ between populations, then genetic variation might be the evolutionary most stable response. If changes happen faster than genetic adaptation, phenotypic plasticity or flexibility can enable an adaptive response. Developmental plasticity provides animals with opportunity to mount a response during their growth phase that is adaptive when they reproduce later as adults. Social flexibility results from the immediate response of individuals to current changing environmental conditions. In contrast to developmental plasticity, social flexibility is reversible and evolves in highly unpredictable environments. In highly predictable environments, plasticity and flexibility are not favoured by natural selection and instead specialisation evolves. Understanding these different processes of intra-specific variation in social organisation will help us to understand the evolution of sociality and adaptability of species.

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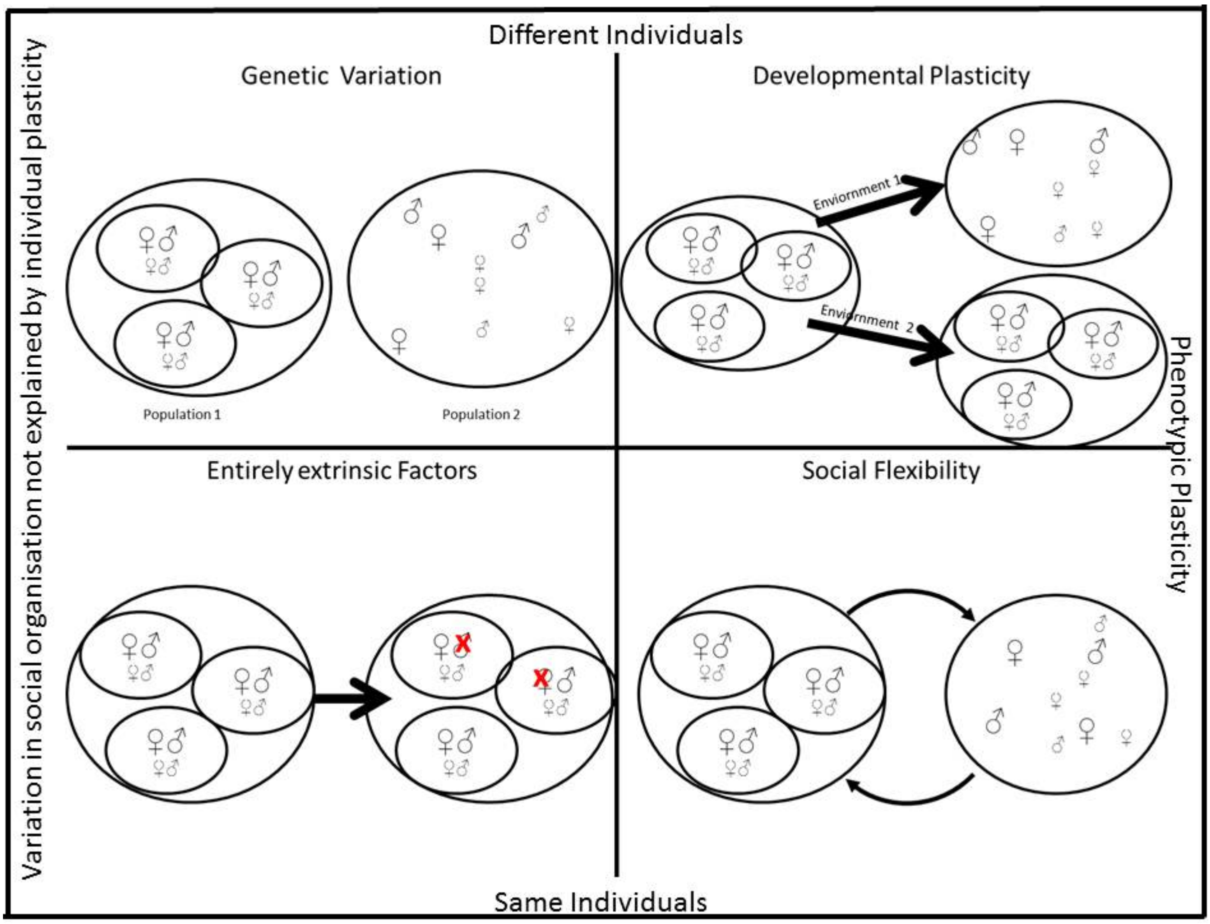

Figure 1. The four processes that can lead to intra-specific variation in social organisation. To explain the variation observed at the population level, we need to consider variation at the individual level. Only the two processes on the right represent phenotypic plasticity.

Top row: different individuals differ in social behaviour. Left, genetic variation: individuals of the same species but two different populations differ genetically, leading to differences in social organisation. Right, developmental plasticity: depending on the environment in which individuals grow up, environmental cues will activate developmental pathways for social behaviour that either leads to the same social organisation as observed in their parent generation (far right bottom) or to a different kind of social organisation (far right top).

Bottom row: the same individuals occur in different forms of social organisation. Left, entirely extrinsic factors: the unpredictable death / disappearance of some breeding individuals is the only cause of changes in social organisation. This itself will cause behavioural flexibility in the survivors, such as mate searching, to return to the original state, but flexibility is the result, not the cause of the observed intra-specific variation in social organisation. Right, social flexibility: if the environment changes, social tactics of individuals change, which as a consequence will change the social organisation of the population. This is reversible, as the same individuals can switch their tactic again, if the environment changes again.

Table 1. Species showing social flexibility.

Species	Male tactics	Female tactics	Social organisations	Fluctuation in population density?	Importance of intra-specific competition	References
Burying beetle ***Nicrophorus vespilloides***	• Attract females via pheromones • Attract females to carcass • Satellite	• Single breeding • Communal breeding • Parasite	• Solitary • Pair-living • One male, multi female	Yes	Carrion size determines number of females that can breed together.	(76-78)
Pied kingfisher ***Ceryle rudis***	• Breeder • Non-reproducing helper • Reproducing helper	• Breeder	• Pair-living • Family group • Two males, one female	Yes	Availability of good nesting sites influences whether un-related helpers are accepted.	(79, 80)
Prairie vole ***Microtus ochrogaster***	• Philopatric helper • Solitary wanderer • Breeder	• Philopatric helper • Single breeder • Communal breeder	• Solitary • Pair-living • Multi male, multi female	Yes (breeding seasons *vs.* winter)	Female-female competition in communally breeding groups: higher reproductive success if only one female breeds per group.	(81-84)

House mouse ***Mus musculus***	• Philopatric helper • Solitary roamer • Breeder	• Philopatric helper • Single breeder • Communal breeder	• Solitary • Pair-living • Multi male, multi female	Yes	Intra-sexual aggression. Female infanticide.	(85, 86)
Striped mouse ***Rhabdomys pumilio***	• Philopatric helper • Solitary roamer • Breeder	• Philopatric helper • Single breeder • Communal breeder	• Solitary • Pair-living • Multi male, multi female	Yes	Intra-sexual aggression. Female infanticide Male reproductive suppression.	(46, 47, 49, 53)

Table 2. Comparison of the four processes that can cause intra-specific variation in social organisation.

	Genetics	**Influence of early environment on behaviour**[2]	**Variability within individuals?**	**Environment in which it evolved**	**Physiological mechanisms**
1. Genetic variation	Polymorphism Narrow reaction norm	No	No	Predictable	Organisational
2. Developmental plasticity	Monomorphism[1] Broad reaction norm	Non-reversible	No	Short term: predictable Long term: unpredictable	Organisational
3. Social flexibility	Monomorphism[1] Broad reaction norm	Reversible	Yes	Unpredictable	Activational
4. Entirely extrinsic factors	Monomorphism[1] Narrow reaction norm	No	Yes	Predictable	None that leads to variation in social organisation

[1]The term genetic monomorphism does not imply that genetic variation is absent, only that the major part of variation observed in social behaviour is not due to genetic but to environmental factors.

[2]Other behaviours can be influenced during early environment, but this cannot explain the variation in social organisation.

Table 3. The predictions to differentiate between the four processes that bring about intra-specific variation in social organisation.

Study	Trait investigated	Yes (trait exists)	No (trait does not exist)
1	**Variability within individuals?**	Social flexibility or extrinsic factors	Genetic variation or developmental plasticity
2	**Genetic polymorphism?**	Genetic variation	Developmental plasticity, social flexibility or extrinsic factors
3	**Early environment can induce changes in individual behaviour**	Developmental plasticity or social flexibility	Genetic variation, extrinsic factors
4	**Alternative forms of social organisation are stable**	Genetic variation, developmental plasticity, or social flexibility	Extrinsic factors
5	**Physiological mechanisms organisational?**	Genetic variation or developmental plasticity	Social flexibility
6	**Predictability of environment in which it evolved**	This factor can change significantly between generations (thus between years, decades or centuries) and is difficult to use for categorisation. Its best used for comparative studies.	

Table 4. Key to determine the process leading to intra-specific variation in social organisation, based on the predictions from Tab. 3. Predictions 5 from Tab. 3 should be used to confirm the results obtained from this key.

No	Question	Result	Go to
1	a Variability occurs within individuals		3
	b Variability does not occur within individuals		2
2	a Genetic polymorphism	**Genetic variation**	
	b Genetic monomorphism	**Developmental plasticity**	
3	a Early environment induces changes in individual behaviour and alternative forms of social organisation are stable	**Social flexibility**	
	b Early environment induces no changes in individual behaviour and alternative forms of social organisation are not stable	**Entirely extrinsic factors**	